# After the long summer: Death and survival of coral communities in the shallow waters of Kume Island, from the Ryukyu Archipelago

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## ARTICLE INFO

## ABSTRACT

Coral reefs in the Ryukyu Islands, southern Japan, have been undergoing degradation for at least five decades. Recently, the archipelago has been hit by bleaching events for two consecutive years (summers of 2016–2017). Shallow coral communities have been reported as especially affected. In this study, using underwater transects, we assessed the status of shallow coral reef communities in Kume Island, at seven distinct locations in Shimajiri Bay, following reports from local fishermen and divers of heavy bleaching across the bay. Our data and analyses revealed that the benthic environment in the bay has algae as the main component, with an average coral cover of only 7.2%. Branching coral colonies, which used to be the most common morphology in Kume Island reefs, accounted for just 7.6% of the total coral cover. Notably, the genus *Acropora* was almost completely absent from our transects, although its recent presence was confirmed by dead colonies making up 4.12% of total transect coverage, suggesting that restoration efforts focused on this genus might be possible in the future. In order for these to be successful, however, a better understanding of the environmental situation at Kume Island is required, including the effects of human activities on coral reef communities.

## 1. Introduction

The Ryukyus, also known as the Nansei Islands, are an archipelago fringed by coral reefs and mangrove forests (Kayanne et al., 2004), located in southern Japan, between Kyūshū and Taiwan, on the direct path of the warm Kuroshio current at subtropical latitudes. The rich marine ecosystems of the Ryukyus provide habitats for over 340 species of scleractinian corals, a number approximately three times higher than that of the Great Barrier Reef at similar latitudes (Nishihira and Veron, 1995). Furthermore, about 70% of the marine biodiversity of Japan may still be undescribed (Fujikura et al., 2010).

Unfortunately, coral reefs in the Ryukyus have been undergoing degradation for at least five decades (Sakai and Nishihira, 1986; Mori, 1995; Omori, 2011) due to multiple factors, including coral predator outbreaks (Sakai and Nishihira, 1986; Omori, 2011), coastal development including land reclamation (Roberts et al., 2002; Omori, 2011; Reimer et al., 2015), pollution (Kawahata et al., 2004; Kitada et al., 2008), sediment runoff (Omori, 2011; Hongo and Yamano, 2013; Fujita et al., 2014; Yamano et al., 2015), overfishing (Nakai, 2002; Kakuma, 2005), storms (Fujita

et al., 2012; Hongo et al., 2012; White et al., 2013), and global climate change (Loya et al., 2001; van Woesik et al., 2011; Hongo et al., 2012; Hongo and Yamano, 2013). Although coral bleaching events are becoming increasingly common, their consequences in terms of coral mortality have varied on a regional basis across the archipelago (Omori, 2011).

Kume Island, or Kume-jima in Japanese (and, hereafter in this paper, Kume) has an area of 59.11 km$^2$ and is located about 90 km west of Okinawa Island, the largest island of the Ryukyu Archipelago. Shimajiri is the biggest bay in Kume and is located in the south-east part of the island (Fig. 1). On the east, the bay is enclosed in a narrow peninsular formation, called "Hate-no-Hama", around 8 km in length. On the north side of Hate-no-Hama, soon after the reef crest, the depth drops sharply to hundreds of meters (Fujita et al., 2012).

Kume hosts a rich marine biodiversity and several endemic species, including critically endangered ones (Ota, 2004; Sato, 2008; Naruse et al., 2012), and the island is included in the Ramsar wetland sites and the World Wildlife Foundation (WWF) list of Biodiversity Priority Areas (Yasumura, 2011; Yamano et al., 2015). However, since the reversion of Okinawa Prefecture to Japan in 1972, Kume, like several other islands in the archipelago, has been affected by significant development, including agriculture and coastal modification, which have significantly altered the

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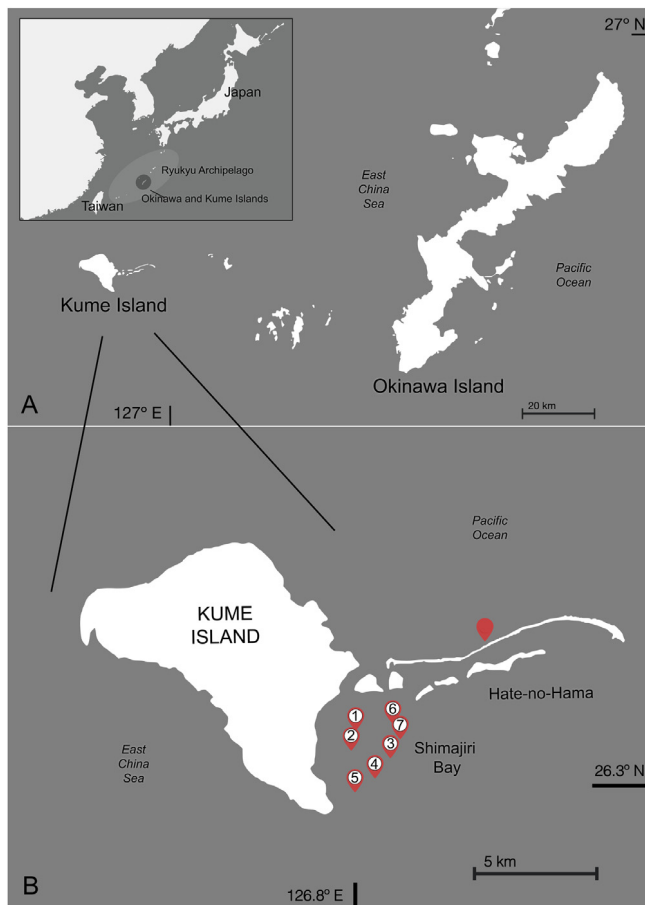   E-mail address: giovannimasucci@me.com (G.D. Masucci).

**Fig. 1.** Kume Island and its surroundings: Okinawa Island, the Ryukyu Archipelago, South Japan, Western Pacific Ocean (A). Survey locations at Shimajiri Bay, Kume Island, Ryukyu Archipelago, Southern Japan (B).

landscape and increased the amount of red soil runoff (Yamano et al., 2015). Red soil, laterite soil with high iron concentrations, is a serious factor in the degradation of Okinawan coral reef ecosystems (West and Van Woesik, 2001; Harii et al., 2014). Sugarcane production, which is one of the main sources of red soil runoff from agriculture in the Ryukyus (Higa et al., 1995), is common across Kume, and has not been effectively managed in the past (Yamano et al., 2015). During the rainy season, red soil in rivers on Kume can reach concentrations up to 2170 mg L$^{-1}$ (Omija et al., 1998).

In 1999, the Kume coral reef community was still described as healthy (Shimoike, 2004). However, bleaching was reported in 2000, with mortality rates of 80% (Shimoike, 2004) and, between 2000 and 2001, 50% of the *Porites* and *Montipora* colonies in Kume died (Shimoike, 2004). Monitoring conducted between 2000 and 2003 by volunteer divers from Reef Check showed coral coverage decreased in two locations on the north shore of the island: from more than 40% to 30% in Akashita at 5 m and from 20% to less than 15% at Hate-no-Hama at 3 m (Shimoike, 2004). Later, Kimura et al. (2011) reported the existence of a healthy and vast community of *Acropora horrida* in the Nanhanari area, in the south of Shimajiri Bay. However, due to the passage of multiple typhoons in summer 2011, large scale destruction of the coral community was reported (Fujita et al., 2012), with coral cover reduced to 25% in the most affected locations and damage extending down to 35 m. No bleaching was reported during the 2011 survey, although the work focused on depths >15 m (Fujita et al., 2012).

Since 2011, no survey results have been published in the scientific literature and the current status of reefs around Kume is unclear. However, local reports of coral bleaching and mortality in 2016 and 2017 raised concerns and prompted Okinawa Prefecture to plan a coral reef restoration effort to be conducted in the near future, by transplanting *Acropora* colonies at depths ≤ 5 m in Shimajiri Bay, as part of a large government effort to restore reefs in Okinawa (Omori et al., 2016; Higa et al., 2018).

Thus, in this study, we assessed the coral and benthic community within Shimajiri Bay in order to document the general health of shallow reefs (≤ 5 m), while examining what coral colony morphologies survived the bleaching events of 2016–2017, and if there were any differences between coral communities at 3 m and 5 m. Our collected data will serve as baseline data in Okinawa Prefecture's efforts to restore genus *Acropora* in the waters of Shimajiri Bay. Branching corals, which used to be the most common morphology in the Ryukyus (Nakano, 2004), have been particularly impacted by thermal stress, leading to phase shifts towards massive and encrusting morphologies across different islands in the region (Loya et al., 2001; van Woesik et al., 2011). Thus, we hypothesized we would find a relatively higher cover of non-branching corals and a lower cover for branching corals. As previous surveys conducted in Kume showed higher coverages at 5 m compared to 3 m (Shimoike, 2004), we hypothesized to find a similar pattern in our surveys. Our collected data will serve as baseline data in Okinawa Prefecture's efforts to restore genus *Acropora* in the waters of Shimajiri Bay.

## 2. Materials and methods

### 2.1. Underwater transects and photograph analyses

The survey was conducted in March 2018. Seven locations were surveyed within Shimajiri Bay using SCUBA and one additional location was surveyed at the north side of Hate-no-Hama (Fig. 1; GPS points: Table 1). For each location, six video transects, one minute each (Anderson et al., 1979; Raymundo et al., 2008), were taken, at 3 and 5 m (three transects per depth per location). Videos were recorded at 4k resolution using wide-angle lenses (Sony SEL16–50 at 16 mm, Sony Corp., Tokyo, Japan) mounted on APS-C cameras (Sony a6300, Sony Corp., Tokyo, Japan). For each video file, six frames were saved, one every 10 s (288 pictures in total). To estimate the benthic community coverage rates, random points were generated (n = 30 per picture, total = 8640 points) using the software Coral Point Count with Excel extension (CPCe 4.1, Kohler and Gill, 2006). Each point was subsequently assigned to a benthic group.

### 2.2. Coral cover and benthic diversity

Benthic groups (11 groups in four categories. Table 2) were analyzed for this study; living branching corals, living non-branching corals, dead corals, algal turf (turf), crustose coralline algae (CCA), macroalgae, sponges, zoantharians, hard carbonate, coral rubble, and sand. In this study, we grouped corals only into functional groups (English et al., 1997; Kohler and Gill, 2006) while also identifying the genus *Acropora*, as this group is the target of Okinawa Prefecture restoration efforts (Zayasu et al., 2018). We included turf, sponges, and zoantharians because these three groups have been implicated in coral reef phase shifts (turf: Swierts and Vermeij, 2016; sponges: Fujii et al., 2011; Reimer et al., 2011a,b; zoantharians: Yang et al., 2013; Cruz et al., 2015) due to a variety of causes, including degrading water quality (Bellwood et al., 2004; Knowlton and Jackson, 2008), eutrophication (Szmant, 2002), and overfishing (Done, 1992; Hughes et al., 2007). While algal turf and macroalgae can be coral competitors

**Table 1**

Latitude and longitude coordinates of the locations examined in this study, and benthic cover %. Abbreviations: SJ = Shimajiri Bay. HNH = Hate-no-Hama, LBC = living branching coral, LNBC = living non-branching corals, LC = total living corals, DC = total dead corals, AT = algal turf, CCA = crustose coralline algae, MA = macroalgae, SPO = sponges, ZOA = zoantharians, HC = hard carbonate, CR = coral rubble, S = Sand.

| Location | GPS | LBC | LNBC | LC | DC | AT | CCA | MA | SPO | ZOA | HC | CR | S |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SJ-1 | 26°19.305N 126°49.365E | 0 | 5.4 | 5.4 | 5.2 | 47.4 | 6.6 | 1.3 | 1.4 | 0.0 | 4.1 | 18.6 | 8.7 |
| SJ-2 | 26°18.901N 126°49.263E | 0.7 | 8.7 | 9.4 | 16.7 | 34.2 | 24.6 | 0.4 | 3.6 | 1.1 | 6.7 | 1.3 | 1.4 |
| SJ-3 | 26°18.712N 126°50.247E | 0.3 | 16.1 | 16.4 | 4.2 | 36.5 | 21.6 | 0.7 | 3.6 | 0.0 | 5.4 | 6.5 | 4.4 |
| SJ-4 | 26°18.243N 126°49.850E | 0.5 | 3.4 | 3.9 | 6.2 | 51.6 | 21.4 | 2.6 | 8.4 | 0.0 | 4.9 | 0.3 | 0.4 |
| SJ-5 | 26°17.916N 126°49.346E | 0.3 | 4.1 | 4.4 | 3.7 | 29.5 | 37.1 | 1.4 | 2.4 | 0.1 | 9.9 | 4.0 | 6.6 |
| SJ-6 | 26°19.382N 126°50.355E | 2.1 | 4.3 | 6.4 | 1.6 | 37.3 | 1.9 | 7.2 | 0.9 | 0.0 | 2.2 | 14.0 | 28.4 |
| SJ-7 | 26°19.137N 26°50.502E | 0 | 4.5 | 4.5 | 6.9 | 39.0 | 12.0 | 0.2 | 0.2 | 0.0 | 2.2 | 20.4 | 13.9 |
| HNH | 26°21.308N 126°52.601E | 1.8 | 10.2 | 12.0 | 1.2 | 25.4 | 52.9 | 1.6 | 0.6 | 0.2 | 2.2 | 3.3 | 0.6 |

**Table 2**

Benthic groups, general categories, and rationale for their inclusion in this study.

| Benthic group | Category | Rationale |
|---|---|---|
| Living branching corals | Coral | Coral health status assessment |
| Living non-branching corals | Coral | Coral health status assessment |
| Dead corals | Coral | Coral health status assessment |
| Algal turf | Algae | Potential coral competitor |
| Crustose coralline algae (CCA) | Algae | Potential available space |
| Macroalgae | Algae | Potential coral competitor |
| Sponges | Other benthic invertebrate | Potential coral competitor |
| Zoantharians | Other benthic invertebrate | Potential coral competitor |
| Hard carbonate | Substrate | Hard substrate, available to corals |
| Coral rubble | Substrate | Non-attached substrate, unsuitable for corals |
| Sand | Substrate | Non-attached substrate, unsuitable for corals |

(Swierts and Vermeij, 2016; van Woesik et al., 2018), coralline algae represent an opportunity for coral colonization as they are considered to be neutral substrate or facilitators (Heyward and Negri, 1999; Ritson-Williams et al., 2010; Gleason and Hofmann, 2011; Doropoulos et al., 2012). van Woesik et al. (2018) found that the amount of macroalgae at a given location could influence the survival rate of transplanted *Acropora* and that the absence of macroalgae was determinant for the survival of the transplants. Finally, while exposed hard carbonate substrates represent an opportunity for coral colonization and growth, incoherent substrates, like loose coral rubble and sand, are generally considered unsuitable for coral settlement and growth, as their inherent instability can negatively affect coral survival, due to the risk of displacement and abrasion damage (Rasser and Riegl, 2002).

### 2.3. Statistical analyses

Statistical tests were performed using R software (version 3.5.1, R Development Core Team, 2018). Multivariate community-based analyses were limited to the seven Shimajiri Bay locations, as only one location at Hate-no-Hama was sampled. Hate-no-Hama data were still included in figures for reference. The different benthic groups were analyzed according to two factors: location (seven levels, corresponding to each sampled location) and depth (two levels: 3 and 5 m). Our analyses examined coral cover, community structure, and substrate composition. As the data departed strongly from normality and contained several zeros, a log+c transformation was performed, according to Ramette (2007), and non-parametric analyses were chosen. For clarity, results are reported untransformed.

Differences in coral cover were tested using PERMANOVA, with the adonis function from the Vegan package for R (version 2.5–2, Anderson, 2001), using Euclidean distance and 9999 permutations. PERMANOVA is a non-parametric test, applicable to uni- and multivariate analyses. While it is mainly used as a multivariate technique, it is also suitable as a non-parametric univariate test (Bakker et al., 2012).

The following biological variables were considered and grouped into the multivariate variable "community": coral cover, turf, CCA, macroalgae, sponges, and zoantharians. Differences in community structure were analyzed with PERMANOVA, using Bray–Curtis as distance method and 9999 permutations. To test the homogeneity of dispersion among groups, all multivariate PERMANOVA tests conducted in this study were further verified using the betadisperser function from the Vegan package for R and a subsequent permutation test (permutest; Legendre et al., 2011). Betadisper is a multivariate analogue of Levene's test for homogeneity of variances (Anderson, 2006). A post-hoc test on the PERMANOVA, with Benjamini and Hochberg (1995) correction, was performed using pairwise.adonis, version 0.2 (Martinez, 2017). Subsequently, multiple comparisons that were significant were analyzed with the Similarity Percent technique (SIMPER, Clarke, 1993), which provides the contribution of each individual variable to the overall Bray–Curtis dissimilarity. The test displays variables that contribute at least to 70% of the differences between each comparison.

In the substrate composition analyses, rubble, sand, and carbonate variables were grouped into the multivariate variable "substrate" (not fauna). Differences in substrate composition were analyzed with PERMANOVA, using Bray–Curtis as distance method and 9999 permutations.
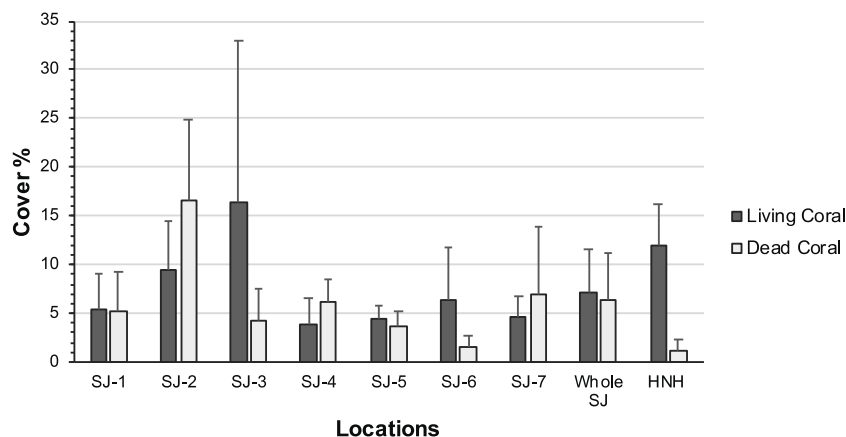
**Fig. 2.** Coral % cover at the surveyed locations. Error bars indicate standard deviations. Abbreviations: SJ = Shimajiri Bay. HNH = Hate-no-Hama.

Finally, an analysis on the patterns of covariance among biological and substrate-related variables was performed. For this, Principal Component Analysis (PCA) was selected, using the rda function from the Vegan package for R (version 2.5–2, Anderson, 2001). PCA results were displayed as a biplot (scaling 2, Gabriel, 1971) with observations (sites x depths) shown as labels and benthic groups as arrows. The directions of the arrows indicate the greatest change in abundance, while the lengths of the arrows indicate the rate of change (Bakker et al., 2012).

## 3. Results

### 3.1. Coral cover

Coral cover at Shimajiri Bay (mean = 7.2%, sd = 7.8%), ranged from a minimum of 3.9% at the Shimajiri-4 location to a maximum of 16.4% at Shimajiri-3 (Fig. 2).

The differences among locations were statistically significant (PERMANOVA, Euclidean distance, permutations = 9999, P = 0.033; Supplementary Table 1). Conversely, depth did not affect coral cover (PERMANOVA, Euclidean distance, permutations = 9999, P = 0.811; Supplementary Table 1) and there were no significant interactions between the factors Depth and Location (PERMANOVA, Euclidean distance, permutations = 9999, P = 0.101; Supplementary Table 1). The survey at Hate-No-Hama found a mean coral cover of 12.0% (Fig. 2). The fraction of branching corals was only 7.6% of the coral cover in Shimajiri Bay and 14.7% of the cover at Hate-no-Hama (Supplementary Fig. 1).

Within Shimajiri Bay, living *Acropora* spp. (Table 3) were only found at one location: Shimajiri-5, at a depth of 5 m, representing only 6.4% of the total coral cover for that location (and 0.28% of the total cover at Shimajiri-5). Overall, *Acropora* spp. cover at Shimajiri was 0.04%, accounting for just 0.56% of the coral cover inside the bay. Conversely, dead *Acropora* colonies were present at all locations, with the highest amount observed at Shimajiri-2 (12.08%, Table 3). At Hate-no-Hama, the cover of living *Acropora* was 0.09%, accounting for 0.8% of the total coral cover for that location.

### 3.2. Benthic community

At Shimajiri Bay, algae were the dominant benthos (mean = 59.2%, sd = 18.8%, Fig. 3). When considering subdivisions within algae (Supplementary Fig. 2), at all locations except one, turf was the most abundant benthic component (mean = 39.4%, sd = 18.8%), followed by CCA (mean = 17.9%, sd = 14.4%), and macroalgae (mean = 2.0%, sd = 3.9%). Within Shimajiri Bay,

**Table 3**
Percent cover for living and dead *Acropora* spp. observed at sites around Kume Island in this study. Abbreviations: SJ = Shimajiri Bay; HNH = Hate-no-Hama.

| Location | 3 m | | 5 m | | Total | |
|---|---|---|---|---|---|---|
| | Living | Dead | Living | Dead | Living | Dead |
| SJ-1 | 0.00 | 1.32 | 0.00 | 5.94 | 0.00 | 3.63 |
| SJ-2 | 0.00 | 18.75 | 0.00 | 5.41 | 0.00 | 12.08 |
| SJ-3 | 0.00 | 3.11 | 0.00 | 1.87 | 0.00 | 2.49 |
| SJ-4 | 0.00 | 5.12 | 0.00 | 2.42 | 0.00 | 3.77 |
| SJ-5 | 0.00 | 3.38 | 0.56 | 1.13 | 0.28 | 2.26 |
| SJ-6 | 0.00 | 0.00 | 0.00 | 1.12 | 0.00 | 0.56 |
| SJ-7 | 0.00 | 2.79 | 0.00 | 5.37 | 0.00 | 4.08 |
| Whole SJ | 0.00 | 4.92 | 0.08 | 3.32 | 0.04 | 4.12 |
| HNH | 0.19 | 0.00 | 0.00 | 0.37 | 0.09 | 0.19 |

Shimajiri-5 was the only location where CCA was the most abundant component. Sponges constituted 2.9% of the benthic cover (sd = 3.6%) and zoantharians 0.2% (sd = 0.6%). At Hate-no-Hama, algae covered 79.9% of our transects with CCA at 52.9%, followed by turf (25.4%) and macroalgae (1.6%). Sponges accounted for 0.6% of the cover and zoantharians for 0.2%.

The composition of the benthic community showed significant differences among locations and depths and interactions between the two factors (PERMANOVA, Bray–Curtis distance method, permutations = 9999, P < 0.001; Supplementary Table 1). Dispersion was homogeneous among groups for Site (permutest, F = 1.7, P = 0.15) and Depth (permutest, F = 2.5; P = 0.13). The post-hoc test highlighted significant differences in community composition for 14 multiple comparisons tests out of a total of 21.

The SIMPER analysis showed that CCA and turf were the variables that most commonly drove differences among locations (Supplementary Fig. 3). CCA was the main contributor to dissimilarity for 11 comparisons and the second largest contributor for three comparisons. Turf was the main contributor for one comparison, the second for eight comparisons and the third largest contributor for five comparisons. Corals were the first largest component for one comparison, the second for two comparisons and the third for three comparisons. Sponges were the first largest component for one comparison, the second for one comparison and the third for two comparisons. Finally, macroalgae helped drive differences between locations for three comparisons, as third largest component. When considering dissimilarity between 3 m and 5 m depths, CCA was the main variable driving differences, followed by turf and corals.

### 3.3. Uncovered substrate and available space

Within Shimajiri Bay, rubble accounted for 9.3% of the total cover, sand for the 9.1%, and hard carbonate for 5.1% (Fig. 4).
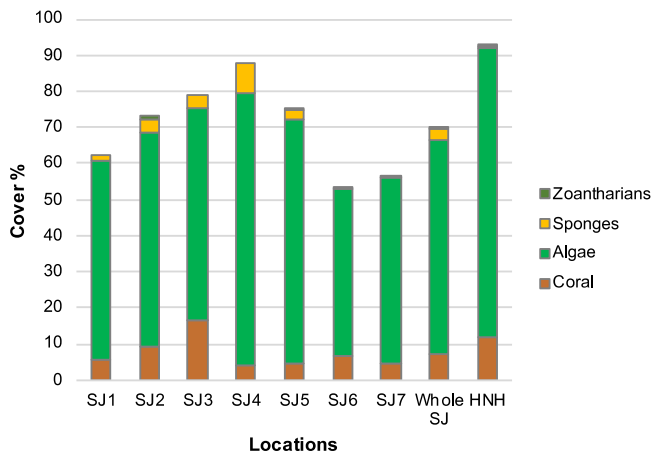
**Fig. 3.** Community composition at the surveyed locations. Abbreviations: SJ = Shimajiri Bay; HNH = Hate-no-Hama.

Shimajiri-6 had the largest amount of uncovered substrate (44.7%), Shimajiri-4 the smallest (5.6%). Uncovered substrate was more common at 5 m than at 3 m (30.4% vs. 16.6%). Overall, uncovered substrate constituted 23.5% of the total cover, with significant differences among locations and depths (PERMANOVA, Bray–Curtis distance method, permutations = 9999, P < 0.001 for Site and Depth, P < 0.01 for Site:Depth; Supplementary

Table 1). However, dispersion was not homogeneous among groups for both Site (permutest, F = 4.26, P = 0.003) and Depth (permutest, F = 6.12; P = 0.019). Hate-no-Hama had only the 6% of its area uncovered (3.3% rubble, 0.6% sand, 2.2% carbonate, Fig. 4). Non-attached substrate, consisting of coral rubble and sand, was more abundant at 5 m.

Considering the area occupied by CCA and hard carbonate as space potentially available for corals, we compared locations in terms of the total available space for corals (the amount of CCA and Hard carbonate, Fig. 4). Shimajiri-5 had the highest amount of available space (47.0%), Shimajiri-6 the lowest amount of available space (41%). Differences among locations and depths were significant (PERMANOVA, Bray–Curtis distance method, permutations = 9999, P ≤ 0.001 for Site and Depth, P < 0.01 for Site:Depth; Supplementary Table 1). Dispersion was homogeneous among groups for Site (permutest, F = 1.03, P = 0.411) and Depth (permutest, F = 1.03; P = 0.403). Hate-no-Hama had 55.1% of the space potentially available for coral colonization, the highest amount among all our examined locations.

### 3.4. Correlations between variables

The PCA biplot did not show clear separation patterns between locations at 3 or 5 m, but highlighted the contribution of turf and CCA to the total variance (Fig. 5) accounting for 82% of the variance in the community. Turf and non-branching corals showed a similar positive covariation pattern, while the
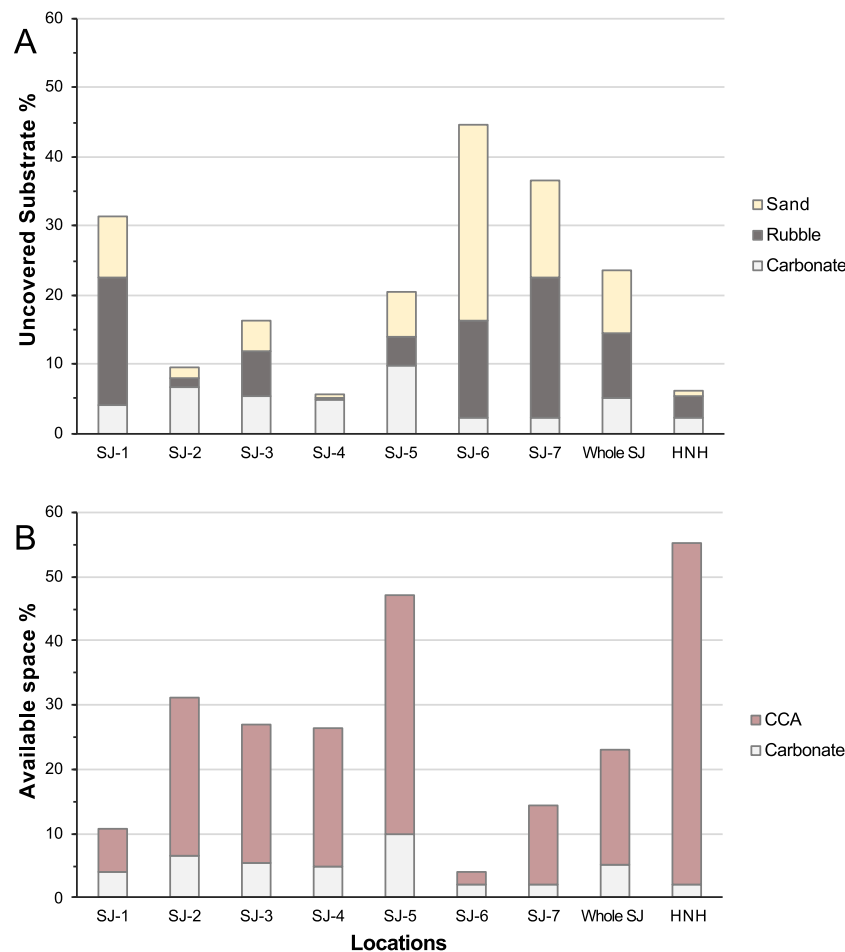


**Fig. 4.** Uncovered substrate at the surveyed locations. Abbreviations: SJ = Shimajiri Bay. HNH = Hate-no-Hama (A). Available space for future coral growth at the surveyed locations. Group abbreviations: CCA = crustose coralline algae. Carbonate = hard carbonate. Locations Abbreviations: SJ = Shimajiri Bay. HNH = Hate-no-Hama (B).
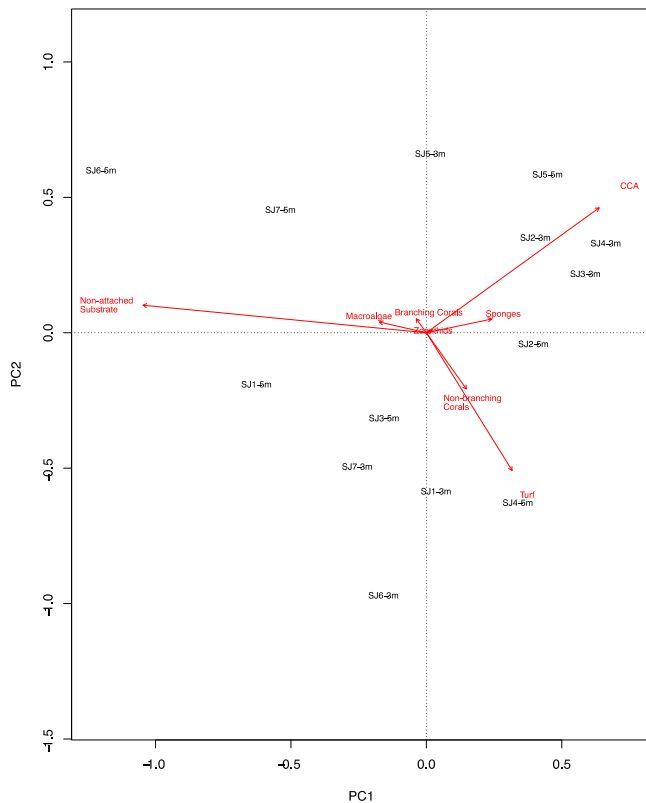
**Fig. 5.** Principal component analysis biplot of the community at Shimajiri Bay. Observations (Site x Depth) are displayed as labels, benthic groups as arrows. The direction of the arrows indicates the greatest change in abundance, the length of the arrows indicates rate of change.

opposite was observed for turf and branching corals. Shimajiri-6 at 5 m showed the highest differences in terms of community composition, mainly driven by high cover of macroalgae (highest among all locations examined). The negative correlation between corals and non-attached substrate was graphically confirmed by the PCA biplot. As well, macroalgae overlapped with non-attached substrate in direction, although the smaller length of the arrow suggests a smaller intensity in its effects.

## 4. Discussion

Shallow coral reefs at Shimajiri Bay are currently not in a 'healthy' state, due to the low living hard coral cover (average: 7.2%), and due to the low diversity of genera and of colony morphologies. As we hypothesized, branching species, once dominant in the Ryukyu Archipelago, and in Shimajiri Bay, were uncommon, making up less than a tenth of the total coral coverage in the bay and thus appear to be the morphological functional group most heavily affected by the coral bleaching events of 2016–2017. These results agree with previous studies in Okinawa in which branching species were "losers" of bleaching events, in contrast with massive and encrusting species (Loya et al., 2001; van Woesik et al., 2011, see also Baskin, 1998 for the first use of the terminology in the context of coral reef ecology). The recent presence of branching corals was confirmed by the several dead *Acropora* colonies observed in our transects. Although each location we examined in Shimajiri Bay showed signs of impact, locations were each affected somewhat differently. Shimajiri-5 had distinctively higher coral coverage and might constitute a source for a future coral recolonization of the bay. Therefore, protection of this location from further impacts should be prioritized.

Results showed a negative covariation between coral cover and non-attached substrate consisting of sand and rubble. Similar results have previously been reported in the literature (Rasser and Riegl, 2002). Increases in the surface covered by rubble can occur following coral degradation (Rasser and Riegl, 2002; Lindahl, 2003; Cameron et al., 2016). What may have happened in Shimajiri Bay is a vicious circle where coral mortality, especially of branching genera, led to an increase in rubble, which in turn made recolonization harder for new coral colonies. The higher presence of non-attached substrate at 5 m, despite the fact that deeper depths should offer advantages in terms of protection from heat, waves, and strong UV light, might be one of the reasons why no differences in coral cover between depths were recorded. We originally hypothesized a higher coral cover at 5 m, but this hypothesis was rejected at our locations in Shimajiri Bay.

The benthic community in Shimajiri Bay was dominated by algae, mainly by algal turf, which is known to be a competitor of coral. Interestingly, at first the PCA analyses revealed that locations with high amounts of turf did not correlate with particularly low coral coverages. We hypothesized that this result could be explained by the fact that turf mainly competes with branching corals, which had a low coverage at all locations in this study, while leaving encrusting and massive coral species less affected (Swierts and Vermeij, 2016). Splitting coral cover in the two distinct variables "branching corals" and "non-branching corals" showed that a negative correlation was present between turf and branching corals, supporting the findings of Swierts and Vermeij (2016).

Within Shimajiri Bay, living colonies of genus *Acropora* were only found at Shimajiri-5, suggesting that this location or Shimajiri-3, the location with the highest coral cover, might be the most suitable for the proposed *Acropora* transplantation to be conducted by Okinawa Prefecture. Shimajiri-2 may also have potential as a candidate for restoration, due to the high coverage of dead *Acropora*. Furthermore, in Shimajiri Bay, these three locations had the highest percentage of available space and the lowest fraction of turf in their algal composition. Although no coral restoration initiative is currently planned at Hate-no-Hama, this area also shows potential, with a high coral coverage, a high percentage of available space, a relatively small fraction of turf, and the presence of living *Acropora*.

The low abundances of branching corals, and *Acropora* in particular, suggest that these components are the ones most in need of restoration efforts. Furthermore, because of their characteristics, such as shape, fast growth rate and asexual reproduction by fragmentation, branching corals have been the most commonly selected candidates for restoration (Rinkevich, 2014). However, the low occurrences in our surveys and the lack of ecological studies describing and quantifying the impacts on marine ecosystems that Kume has been facing over the last decades, and potentially is still facing today, suggest that caution is needed. The understanding and elimination, or at least mitigation, of stress factors, is considered to be the minimum requirement for a successful reef restoration initiative (Omori, 2011). Future studies should focus on obtaining more knowledge on the area by adding benthic (e.g. more coral genera in addition to *Acropora*) and non-benthic groups, like fish communities. Coral recruitment should also be evaluated in order to better understand recovery potential. Efforts to quantify and mitigate local impacts should also be at the center of future research and conservation strategies, in collaboration with Okinawa Prefecture. For example, the impact of red soil on shallow coral reefs communities should not be underestimated. Although laws have been set to reduce runoff, high levels of red soil are still present, due to public works construction, coastal modifications, deforestation, and agriculture (Yamano et al., 2015). The levels of red soil in the water at the surveyed locations should be considered in any final site evaluation

and monitored regularly and frequently, before, during, and after the coral restoration effort. In addition, more effective legislation and good management practices should be enforced to reduce red soil impact on the bay ecosystem. Although climate change is an obvious stress factor, soil runoff, construction, aquaculture, and overfishing should be investigated in order to fully understand the reasons that led to the current situation in Shimajiri Bay and the measures needed to implement an effective reef restoration strategy. Finally, the institution of a marine protected area (MPA) could be a powerful tool to grant protection both to the surviving corals and to the colonies to be transplanted in the future.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2019.100578.

## References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253.

Anderson, D.R., Laake, J.L., Crain, B.R., Burnham, K.P., 1979. Guidelines for line transect sampling of guidelines biological. J. Wildlife Manag. 43 (1), 70–78.

Bakker, J.D., Colasurdo, L.B., Evans, J.R., 2012. Enhancing Garry oak seedling performance in a semiarid environment. Northwest Sci. 86 (4), 300–309.

Baskin, Y., 1998. Winners and losers in a changing world. Bioscience 48, 788–792.

Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. Nature 429 (6994), 827–833.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. Ser. B Stat. Methodol. 57, 289–300, http://www.jstor.org/stable/2346101.

Cameron, C.M., Pausch, R.E., Miller, M.W., 2016. Coral recruitment dynamics and substrate mobility in a rubble-dominated back reef habitat. Bull. Mar. Sci. 92 (1), 123–136. http://dx.doi.org/10.5343/bms.2015.1030.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Cruz, I.C., Loiola, M., Albuquerque, T., Reis, R., José de Anchieta, C.C., Reimer, J.D., Mizuyama, M., Kikuchi, R.K., Creed, J.C., 2015. Effect of phase shift from corals to zoantharia on reef fish assemblages. PLoS One 10 (1), e0116944.

Done, T.J., 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247, 121–132.

Doropoulos, C., Ward, S., Diaz-Pulido, G., Hoegh-Guldberg, O., Mumby, P.J., 2012. Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. Ecol. Lett. 15, 338–346.

English, S., Wilkinson, C., Baker, V., 1997. Survey Manual for Tropical Marine Resources, second ed. Australian Institute of Marine Science, Townsville.

Fujii, T., Keshavmurthy, S., Zhou, W., Hirose, E., Chen, C.A., Reimer, J.D., 2011. Coral-killing cyanobacteriosponge Terpios hoshinota on the Great Barrier Reef. Coral Reefs 30, 483–483.

Fujikura, K., Lindsay, D., Kitazato, H., Nishida, S., Shirayama, Y., 2010. Marine biodiversity in Japanese waters. PLoS One 5 (8), http://dx.doi.org/10.1371/journal.pone.0011836.

Fujita, Y., Kimura, T., Shioiri, A., Naruse, T., 2012. Typhoon damage of large-scaled coral communities dominated by Acropora horrida Dana, 1846 Scleractinia: Acroporidae in the mesophotic zone off Kumejima Island, the Ryukyu Islands, Japan. Biol. Mag. Okinawa 50, 61–66, (in Japanese).

Fujita, K., Nagamine, S., Ide, Y., Umezawa, Y., Hosono, T., Kay-anne, H., Yamano, H., 2014. Distribution of large benthic foraminifers around a populated reef island: Fongafale Island, Funafuti Atoll, Tuvalu. Mar. Micropaleontol. 113, 1–9.

Gabriel, K.R., 1971. The biplot graphical display of matrices with application to principal component analysis. Biometrika 58, 453–467.

Gleason, D.F., Hofmann, D.K., 2011. Coral larvae: From gametes to recruits. J. Exp. Mar. Biol. Ecol. 408, 42–57.

Harii, S., Hongo, C., Ishihara, M., Ide, Y., Kayanne, H., 2014. Impacts of multiple disturbances on coral communities at Ishigaki Island, Okinawa, Japan, during a 15 year survey. About Mar. Ecol.-Progr. Ser. 509, 171–180.

Heyward, A.J., Negri, A.P., 1999. Natural inducers for coral larval metamorphosis. Coral Reefs 18, 273–279.

Higa, E., Omija, T., Hanashiro, K., Mitsumoto, H., 1995. Quantity of soil run-off on okinawa island. In: Annual Report Okinawa Prefecture Department of Health and Environment, Vol. 29. pp. 83–88.

Higa, Y., Shinzato, C., Zayasu, Y., Nagata, T., Nakamura, R., Yokokura, A., Janadou, S., Omori, M., 2018. Flexible development of techniques for coral reef restoration using asexual reproduction in the Coral Reef Preservation and Rehabilitation Project by Okinawa Prefectural Government, Japan. J. Jpn. Coral Reef Soc. 20 (1), 21–37.

Hongo, C., Kawamata, H., Goto, K., 2012. Catastrophic impact of typhoon waves on coral communities in the Ryukyu Islands under global warming. J. Geophys. Res.: Biogeosci. 117 (2), http://dx.doi.org/10.1029/2011JG001902.

Hongo, C., Yamano, H., 2013. Species-specific responses of corals to bleaching events on anthropogenically turbid reefs on Okinawa Island, Japan, over a 15-year period (1995-2009). PLoS One 8 (4), http://dx.doi.org/10.1371/journal.pone.0060952.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr. Biol. 17, 360–365.

Kakuma, S., 2005. Coastal fisheries co-management in okinawa, samoa and the philippines with fish aggregating devices as sources of alternative income. Senri Ethnol. Stud. 67, 197–214.

Kawahata, H., Ohta, H., Inoue, M., Suzuki, A., 2004. Endocrine disrupter nonylphenol and bisphenol A contamination in Okinawa and Ishigaki Islands, Japan - within coral reefs and adjacent river mouths. Chemosphere 55 (11), 1519–1527. http://dx.doi.org/10.1016/j.chemosphere.2004.01.032.

Kayanne, H., Hongo, C., Yamano, H., 2004. Coral reef landforms in Japan. In: Coral Reefs of Japan (Ministry of the Environment, Japanese Coral Reef Society, eds). Ministry of the Environment, Japan, Tokyo, pp. 14–19, (Chapter 1).

Kimura, T., Shimoike, K., Suzuki, G., Nakayoshi, I., Shioiri, A., Tabata, A., Tabata, Y., Fujita, Y., Zayasu, Y., Yamano, H., Namizaki, N., 2011. Large scale communities of Acropora horrida in the mesophotic zone off Kume Island, Okinawa. J. Jpn. Coral Reef Soc. 13, 43–45.

Kitada, Y., Kawahata, H., Suzuki, A., Oomori, T., 2008. Distribution of pesticides and bisphenol a in sediments collected from rivers adjacent to coral reefs. Appl. Catal. B 82 (3–4), 163–168.

Knowlton, N., Jackson, J.B., 2008. Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol. 6, e54.

Kohler, K.E., Gill, S.M., 2006. Coral point count with excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. Comput. Geosci. 32 (9), 1259–1269.

Legendre, P., Oksanen, J., ter Braak, C.J.F., 2011. Testing the significance of canonical axes in redundancy analysis. Methods Ecol. Evol. 2, 269–277.

Lindahl, U., 2003. Coral reef rehabilitation through transplantation of staghorn corals: effects of artificial stabilization and mechanical damages. Coral Reefs 22 (3), 217–223.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., van Woesik, R., 2001. Coral bleaching: the winners and the losers. Ecol. Lett. 4 (2), 122–131.

Martinez, Arbizu P., 2017. pairwiseAdonis: Pairwise Multilevel Comparison using Adonis. R Package Version 0.0.1.

Mori, M., 1995. Movement of stony corals and crown-of-thorns starfish in Sekisei Lagoon. Mar. Parks J. 107, 10–15, (in Japanese).

Nakai, T., 2002. Management of fishery resources for groupers (Serranidae) in Okinawa, southern Japan. Fish. Sci. 68, 431–432.

Nakano, Y., 2004. Global environmental change and coral bleaching. In: Coral Reefs of Japan (Ministry of the Environment, Japanese Coral Reef Society, eds). Ministry of the Environment, Japan, Tokyo, pp. 42–48, (Chapter 2).

Naruse, T., Chan, T.Y., Tan, H.H., Ahyong, S.T., Reimer, J.D., 2012. Scientific results of the kumejima marine biodiversity expedition—KUMEJIMA 2009. Zootaxa 3367 (1), 5–7.

Nishihira, M., Veron, J.E.N., 1995. Hermatypic Corals of Japan. Kaiyusha, Tokyo, p. 439pp, (in Japanese).

Omija, T., Higa, E., Nakasone, K., Mitsumoto, H., 1998. Effect of soil run-off on SS of river water in Okinawa Island and Kume Island. In: Annual Report Okinawa Prefecture Department of Health and Environment, Vol. 32. pp. 149–159.

Omori, M., 2011. Degradation and restoration of coral reefs: Experience in Okinawa, Japan. Mar. Biol. Res. 7 (1), 3–12. http://dx.doi.org/10.1080/17451001003642317.

Omori, M., Higa, Y., Shinzato, C., Zayasu, Y., Nagata, T., Nakamura, R., Yokokura, A., Janadou, S., 2016. Development of active restoration methodologies for coral reefs using asexual reproduction in Okinawa, Japan. In: Proceedings of the 13th International Coral Reef Symposium. pp. 369–387.

Ota, H., 2004. Field observations on a highly endangered snake, Opisthotropis kikuzatoi (Squamata: Colubridae), endemic to Kumejima Island, Japan. Curr. Herpetol. 23, 73–80.

R Development Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Ramette, A., 2007. Multivariate analyses in microbial ecology. FEMS Microbiol. Ecol. 62 (2), 142–160. http://dx.doi.org/10.1111/j.1574-6941.2007.00375.x.

Rasser, M., Riegl, B., 2002. Holocene coral reef rubble and its binding agents. Coral Reefs 21 (1), 57–72. http://dx.doi.org/10.1007/s00338-001-0206-5.

Raymundo, L.J., Couch, C.S., Harvell, C.D., Raymundo, J., Bruckner, A.W., Work, T.M., Weil, E., Woodley, C.M., Jordan-Dahlgren, E., Willis, B.L., Sato, Y., Aeby, G.S., 2008. Coral disease handbook. In: Guidelines for Assessment, Monitoring & Management.

Reimer, J.D., Mizuyama, M., Nakano, M., Fujii, T., Hirose, E., 2011a. Current status of the distribution of the coral-encrusting cyanobacteriosponge Terpios hoshinota in southern Japan. Galaxea 131, 35–44.

Reimer, J.D., Nozawa, Y., Hirose, E., 2011b. Domination and disappearance of the black sponge: a quarter century after the initial Terpios outbreak in southern Japan. Zool. Stud. 50, 394.

Reimer, J.D., Yang, S.Y., White, K.N., Asami, R., Fujita, K., Hongo, C., Ito, S., Kawamura, I., Maeda, I., Mizuyama, M., Obuchi, M., Sakamaki, T., Tachihara, K., Tamura, M., Tanahara, A., Yamaguchi, A., Jenke-Kodama, H., 2015. Effects of causeway construction on environment and biota of subtropical tidal flats in Okinawa, Japan. Mar. Pollut. Bull. 94 (1–2), 153–167. http://dx.doi.org/10.1016/j.marpolbul.2015.02.037.

Rinkevich, B., 2014. Rebuilding coral reefs: does active reef restoration lead to sustainable reefs?. Curr. Opin. Environ. Sustain. 7, 28–36.

Ritson-Williams, R., Paul, V.J., Arnold, S.N., Steneck, R.S., 2010. Larval settlement preferences and post-settlement survival of the threatened Caribbean corals Acropora palmata and A. cervicornis. Coral Reefs 29, 71–81.

Roberts, C.M., McClean, C.J., Veron, J.E., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C., Werner, T.B., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295 (5558), 1280–1284.

Sakai, K., Nishihira, M., 1986. Ecology of hermatypic corals. In: Nishihira, M. (Ed.), Coral Reefs of Okinawa. Okinawa Environmental Analysis Center Co. Ltd, Urasoe City, pp. 83–97, (in Japanese).

Sato, F., 2008. Occurrence dynamics of Luciola owadai (2001-2007). In: Proceedings of Kumejima Museum, Vol. 8. pp. 47–63.

Shimoike, K., 2004. Iheya, izena, aguni, tonaki, and kume islands. In: Coral Reefs of Japan (Ministry of the Environment, Japanese Coral Reef Society, eds). Ministry of the Environment, Japan, Tokyo, pp. 190–193, (Chapter 6).

Swierts, T., Vermeij, M.J., 2016. Competitive interactions between corals and turf algae depend on coral colony form. PeerJ 4, e1984. http://dx.doi.org/10.7717/peerj.1984.

Szmant, A.M., 2002. Nutrient enrichment on coral reefs: is it a major cause of coral reef decline?. Estuaries 25, 743–766.

West, K., Van Woesik, R., 2001. Spatial and temporal variance of river discharge on Okinawa (Japan): inferring the temporal impact on adjacent coral reefs. Mar. Pollut. Bull. 42, 864–872.

White, K.N., Ohara, T., Fujii, T., Kawamura, I., Mizuyama, M., Montenegro, J., Shikiba, H., Naruse, T., McClell, T., Denis, V., Reimer, J.D., 2013. Typhoon damage on a shallow mesophotic reef in Okinawa, Japan. PeerJ 1, e151. http://dx.doi.org/10.7717/peerj.151.

van Woesik, R., Ripple, K., Miller, S.L., 2018. Macroalgae reduces survival of nursery-reared Acropora corals in the Florida reef tract. Restor. Ecol. 26 (3), 563–569.

van Woesik, R., Sakai, K., Ganase, A., Loya, Y., 2011. Revisiting the winners and the losers a decade after coral bleaching. Mar. Ecol. Prog. Ser. 434, http://dx.doi.org/10.3354/meps09203.

Yamano, H., Satake, K., Inoue, T., Kadoya, T., Hayashi, S., Kinjo, K., Nakajima, D., Oguma, H., Ishiguro, S., Okagawa, A., Suga, S., Horie, T., Nohara, K., Fukayama, N., Hibiki, A., 2015. An integrated approach to tropical and subtropical island conservation. J. Ecol. Environ. 38 (2), 271–279. http://dx.doi.org/10.5141/ecoenv.2015.028.

Yang, S.Y., Bourgeois, C., Ashworth, C.D., Reimer, J.D., 2013. Palythoa zoanthid 'barrens' in Okinawa: examination of possible environmental causes. Zool. Stud. 52, 39.

Yasumura, S. (Ed.), 2011. WWF Japan Nansei Islands Biological Diversity Evaluation Project Report. WWF Japan, Tokyo.

Zayasu, Y., Satoh, N., Shinzato, C., 2018. Genetic diversity of farmed and wild populations of the reef-building coral, Acropora tenuis. Restor. Ecol. 119, 5–1202. http://dx.doi.org/10.1111/rec.12687.